AMERICAN MUSEUM
*Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3548, 22 pp., 12 figures, 12 tables January 15, 2007

# Geographic Variation of *Idiurus* (Rodentia: Anomaluridae) with Emphasis on Skull Morphometry

ANJA C. SCHUNKE[1] AND RAINER HUTTERER[2]

## ABSTRACT

The geographic variation of skull size and shape among populations of flying squirrels of the genus *Idiurus* was analyzed with multivariate techniques using up to 57 craniometric characters. The variability of body size and fur coloration was also studied. The results support the present division of the genus into two species, *Idiurus macrotis* and *I. zenkeri*. Further division, into subspecies, does not seem to be warranted at present, although distinguishable geographical populations exist in West, Central, and East Africa.

## INTRODUCTION

Anomaluridae are small to large rodents restricted to equatorial Africa between latitudes 15°N and 15°S. All except one species, *Zenkerella insignis*, are able to perform gliding flight. All anomalurids live in rain forest, montane forest, or gallery forest. High trees provide takeoff and landing sites for glides and provide hollows for the daytime rest. As anomalures are nocturnal and seldom maintained in captivity, very little is known about their biology (Durrell, 1952; Rahm, 1969; Schlitter 1989; Julliot et al., 1998).

Seven species of Anomaluridae are currently recognized (Dieterlen, 1993, 2005) and placed in three or four genera: *Anomalurus* (which occasionally contains *Anomalurops*), *Zenkerella*, and *Idiurus*.

Most current authors agree that *Idiurus* consists of two species, *I. macrotis* and *I. zenkeri* (Misonne, 1971; Rahm, 1988; Nowak, 1991; Dieterlen, 1993, 2005). They are the smallest members of the family, with head and body lengths ranging from about 95 mm in *I. macrotis* to about 75 mm in *I. zenkeri*. These animals have a gliding membrane supported by a cartilaginous rod extending from the elbow

[1] Zoologisches Forschungsmuseum Alexander Koenig, 53113 Bonn (a.schunke.zfmk@uni-bonn.de).
[2] Division of Vertebrate Zoology (Mammalogy), American Museum of Natural History; and Zoologisches Forschungsmuseum Alexander Koenig, 53113 Bonn (r.hutterer.zfmk@uni-bonn.de).

 ISSN 0003-0082

and a long, sparsely haired tail that considerably exceeds the head and body length.

A preliminary analysis of the distributions of both species (Schunke and Hutterer, 2000) revealed that large continuous distributions across the Central African forest belt, as postulated by some authors (e.g. Kingdon, 1997), were not supported by specimen-based distribution maps, which in contrast suggest patchy distributions for both species. Geographical isolation may cause genetic drift and result in speciation of populations of these arboreal rodents. To test this hypothesis, we have analyzed the morphological variation among geographical populations of *Idiurus* species across their entire range from Sierra Leone in the west to Tanzania in the east.

## SPECIMENS AND METHODS

Specimens in 14 museum collections form the basis of our report. In total, we examined 116 *Idiurus macrotis* and 83 *I. zenkeri* (appendix 1). Of these, craniometric data taken from 63 skulls of *I. macrotis* and 51 skulls of *I. zenkeri* were used for the calculations. Only skulls with all molars completely emerged were used in order to exclude juveniles. From each skull, up to 57 measurements were taken with an electronic caliper to the nearest 0.01 mm (fig. 1, table 1).

Variation in color was assessed in a sample of 55 skins of *I. macrotis* and 41 skins of *I. zenkeri*; color slides showing the skins along with a color reference were used for comparison.

The specimens originated from the entire ranges of the two species (figs. 2–3). We defined six geographical clusters and used them as operational units:

1. WA: West Africa (Sierra Leone, Ivory Coast, and Ghana; *I. macrotis* only).
2. NWC: Northwestern Cameroon.
3. CEG: Southern Cameroon, Equatorial Guinea, and Gabon.
4. CAR: Central African Republic (*I. zenkeri* only).
5. DRC: Democratic Republic of Congo.
6. TAN: Tanzania (*I. macrotis* only).

The two species were analyzed separately. Measurements were converted to logarithms before entering the calculations. The normal distribution of the data was tested with a Kolmogorov-Smirnov test independently for both species. For this test, specimens from the northeastern part of the Democratic Republic of Congo were used because the largest numbers of specimens were available from this area. The same subsets were also tested for sexual dimorphism with t-tests (with the exclusion of specimen of unknown sex).

For the main analysis, the remaining data were submitted to a principal component analysis (PCA). Two PCAs were conducted. The first was based on the ln-transformed absolute measurements and thus included variation in size. In the second analysis, linear regression lines of individual ln-transformed measurements on ln-transformed palatilar length (PL, fig. 1) were calculated, and residuals of the individual measurements on this line were used instead of original variables (Thorpe and Leamy, 1983) to compare only shape differences. Palatilar length was chosen as reference because of its relatively high values (and thus relatively low measuring error) and for its availability from most specimens.

In addition, a PCA was performed for standard body measurements (collectors' field data), including total length, tail length, ear length, and hind-foot length (appendix 2). Total length was taken as combined tail length and head and body length, where necessary. Residuals were calculated for the hind-foot length.

After grouping the populations according to the results of the PCA (see later), a discriminant analysis was conducted to specify differences between groups.

As *Idiurus* skulls are very fragile, it was rarely possible to take all measurements from a single skull. Therefore, the PCA was conducted first with all characters and then repeated after a stepwise exclusion of measurements that were unavailable for several specimens. While the number of specimens increased, the number of characters decreased. By comparing the results, it was possible to test their robustness.

Examples of typical results with intermediate numbers of characters and specimens are shown in scatter plots for the first and second principal component, or in box plots. Calculations were processed with the program SPSS (version 10.0).

Additional statistical details are given in appendix 3, tables 8–12.

## INSTITUTIONAL ABBREVIATIONS

| | |
|---|---|
| AMNH | American Museum of Natural History, New York |
| BMNH | British Museum of Natural History, London |
| FMNH | Field Museum of Natural History, Chicago |
| MNHN | Muséum National d'Histoire Naturelle, Paris |
| MRAC | Museum Royal d'Afrique Centrale, Tervuren |
| NHMB | Naturhistorisches Museum, Basel |
| NMK | National Museums of Kenya, Nairobi |
| NMNH | National Museum of Natural History, Washington, DC |
| NMW | Naturhistorisches Museum, Vienna |
| NRM | Naturhistoriska Riksmuseet, Stockholm |
| RMNH | Nationaal Natuurhistorisch Museum (Naturalis), Leiden |
| SMF | Forschungsinsitut Senckenberg, Frankfurt |
| SMNS | Staatliches Museum für Naturkunde, Stuttgart |
| ZMB | Museum für Naturkunde, Berlin |

## RESULTS

### Normal Distribution

All measurements were normally distributed in both species ($p > 0.05$).

### Sexual Dimorphism

The possibility of sexual dimorphism was checked independently for logarithmized measurements and for residuals for palatilar length. Thirteen characters demonstrated significant (t-test, $p \leq 0.05$) intersexual differences for at least one of the species. Although preliminary tests with all characters yielded similar results, those characters were not used in the final analyses. Their exclusion made it possible to use all specimens in a single analysis and to include skulls of specimens with unknown sex to maximize the sample size.

### Principal Component Analyses

After the removal of 13 characters, the remaining 44 characters underwent a PCA. Within *I. macrotis*, four clusters were formed by the first and second principal component for logarithmized absolute data (fig. 4, table 8). The first factor codes mainly for size differences. The smallest specimens came from West Africa and from northwestern Cameroon, while specimens from southern Cameroon, Equatorial Guinea, and Gabon were considerably larger. Animals from northeastern Democratic Republic of Congo were intermediate in size, with a slight overlap in one or both directions. A single specimen from Tanzania (NMW 31089) is larger than average values of series from southern Cameroon to Gabon but does not exceed the range of variation in most characters. Unfortunately, no other skulls from the Tanzanian population are available.

The second principal component demonstrates differences in shape rather than size. It separates specimens from West Africa and northwestern Cameroon, on one hand, and animals from the Democratic Republic of Congo and southern Cameroon to Gabon, on the other.

Calculations using the residuals for palatilar length gave basically the same pattern but were less pronounced than those obtained from logarithmized absolute measurements. Here the single skull from Tanzania clustered in most plots within specimens from southern Cameroon to Gabon.

Results for *I. zenkeri* are less pronounced (fig. 5, table 9). No size differences between specimens from different localities could be detected with the first principal component. With the second principal component, a separation (with some overlap) was possible between individuals from southern Cameroon and Equatorial Guinea and northeastern Democratic Republic of Congo. The holotype of *zenkeri* from Cameroon (BMNH 48.885) has a slightly smaller skull than most other conspecifics from other localities. Further reduction of the number of characters demonstrated that a second specimen (BMNH 48.886) from Cameroon was even smaller (not shown in fig. 5). From the Central African Republic only two skulls were available, one slightly and the other considerably damaged. With a strongly reduced number of characters, they clustered either with the Cameroon and Equatorial Guinea population or held an

TABLE 1
**Cranial and Dental Measurements Taken from Skulls of *Idiurus macrotis* and *I. zenkeri***
0: character not used in final PCA; 1 and 2: character used in analyses; 2: character used in figs. 4 to 7. Abbreviations as in fig. 1.

| Code | Measurement | *I. macrotis* | *I. zenkeri* | Both species |
|---|---|---|---|---|
| TL | Total length | 0 | 0 | 0 |
| CIL | Condylo-incisive length | 1 | 1 | 1 |
| BL | Basal length | 2 | 1 | 1 |
| ZB | Zygomatic breadth | 1 | 1 | 1 |
| RB | Breadth of rostrum | 2 | 1 | 1 |
| NB | Breadth of nasal bones | 0 | 0 | 0 |
| IOB | Interorbital breadth | 2 | 2 | 2 |
| BCB | Breadth of braincase | 2 | 1 | 1 |
| PL | Palatilar length | 2 | 2 | 2 |
| PPBL | Postpalatine basal length | 1 | 1 | 1 |
| DL | Length of diastema | 0 | 0 | 0 |
| FIL | Length of incisive foramen | 1 | 2 | 1 |
| FIB | Width of incisive foramen | 2 | 2 | 2 |
| BP4 | Gum width at P4 | 2 | 2 | 2 |
| BM1 | Gum width at M1 | 2 | 2 | 2 |
| BM3 | Gum width at M3 | 0 | 0 | 0 |
| ChB | Width of choana | 2 | 2 | 2 |
| Bulla L | Length of bulla | 2 | 2 | 2 |
| Bulla B | Width of bulla | 2 | 2 | 2 |
| RH | Heigth of rostrum | 2 | 2 | 2 |
| ZH | Height of zygomatic arc | 0 | 0 | 0 |
| PFZ H | Height of processus frontalis zygomatici | 0 | 0 | 0 |
| SkH | Height of skull | 0 | 0 | 0 |
| ZP | Position of zygomatic arc | 0 | 0 | 0 |
| BCH | Height of braincase | 0 | 0 | 0 |
| PZB | Width across posterior ends of zygomatic arcs | 2 | 2 | 2 |
| FIO H | Height of infraorbital foramen | 2 | 2 | 2 |
| FIO B | Width of infraorbital foramen | 2 | 2 | 2 |
| RUL | Upper length of rostrum | 2 | 2 | 2 |
| RLL | Lower length of rostrum | 2 | 2 | 2 |
| ML | Length of mandible | 2 | 2 | 2 |
| MHA | Height of mandible at articular process | 2 | 2 | 2 |
| MHD | Height of mandible at diastema | 0 | 0 | 0 |
| PAA | Distance between articular and angular process | 2 | 1 | 1 |
| PCH | Height of coronoid process | 2 | 2 | 2 |
| UCL | Upper crown length of molars | 1 | 1 | 1 |
| UIL | Length of upper incisor | 2 | 2 | 2 |
| UIB | Width of upper incisor | 2 | 2 | 2 |
| UP4L | Length of upper P4 | 1 | 1 | 1 |
| UP4B | Width of upper P4 | 1 | 1 | 1 |
| UM1L | Length of upper M1 | 0 | 0 | 0 |
| UM1B | Width of upper M1 | 1 | 1 | 1 |
| UM2L | Length of upper M2 | 1 | 1 | 1 |
| UM2B | Width of upper M2 | 1 | 1 | 1 |
| UM3L | Length of upper M3 | 1 | 1 | 1 |
| UM3B | Width of upper M3 | 1 | 1 | 1 |
| LCL | Lower crown length of molars | 2 | 1 | 1 |
| LIL | Length of lower incisor | 2 | 2 | 2 |
| LIB | Width of lower incisor | 2 | 2 | 2 |
| LP4L | Length of lower P4 | 1 | 1 | 1 |
| LP4B | Width of lower P4 | 1 | 1 | 1 |

TABLE 1
*(Continued)*

| Code | Measurement | *I. macrotis* | *I. zenkeri* | Both species |
|---|---|---|---|---|
| LM1L | Length of lower M1 | 1 | 1 | 1 |
| LM1B | Width of lower M1 | 1 | 1 | 1 |
| LM2L | Length of lower M2 | 0 | 0 | 0 |
| LM2B | Width of lower M2 | 1 | 1 | 1 |
| LM3L | Length of lower M3 | 0 | 0 | 0 |
| LM3B | Width of lower M3 | 1 | 1 | 1 |

intermediate position, depending on the number of characters and individuals included in the respective analyses.

Calculations with residuals gave remarkably similar results to the ones obtained with logarithmized absolute measurements.

Size differences between *I. macrotis* and *I. zenkeri* were pronounced, with a considerable gap in the first principal component (fig. 6, table 10); they were strongly supported by the majority of characters.

An interesting result was obtained from a combined analysis for *I. macrotis* and *I. zenkeri* using residuals for palatilar length (fig. 7, table 10). While the first principal component (not shown) mainly separated *I. macrotis* from northwestern Cameroon and the southern Cameroon to Gabon region, but less clearly animals from West Africa and the Democratic Republic of Congo, the analysis yielded no information as to *I. zenkeri.*

However, the second principal component divided the specimens in individuals from Democratic Republic of Congo and animals from southern Cameroon to Gabon, with a considerable overlap between *I. macrotis* and *I. zenkeri* from the respective areas. The characters demonstrating high loadings at this principal axis were length and width of the bulla, upper length of rostrum, and two incisor characters.

## Discriminant Analysis

Most individuals of the clusters obtained through the PCA analysis could be identified with only few characters. More than 90% of specimens were classified correctly. In populations of *I. macrotis*, a combination of four characters (height of rostrum, length of bulla, length of mandible, and distance between articular and angular process) yielded 94.2% correct classifications (tables 2, 11). However, the results for specimens from northwestern Cameroon must be taken with caution, as only five skulls were available from this area.

The discriminant analysis gave similar results for *I. zenkeri* populations, with 94.9% correctly classified individuals (tables 3, 12). The characters used were height of rostrum, width of bulla, and upper and lower rostrum length. Unfortunately, only specimens from southern Cameroon plus Equatorial Guinea and the Democratic Republic of Congo yielded a sufficient number of measurements and could be used in this analysis.

*I. macrotis* and *I. zenkeri* may be separated from each other by a single character, such as height of rostrum, basal length, or palatilar length. Each of these characters correctly classified 100% of the specimens in a discriminant analysis.

Tables 4 and 5 provide means and ranges of five selected skull measurements of the different geographical populations of each species, and figures 8–10 show examples of crania of both species. Skulls of all holotype specimens are figured, with the exception of *kivuensis* Lönnberg, 1917, the skull of which is lost.

## Body Size and Skin Characters

A PCA for total length, tail length, ear length, and hind-foot length (field measurements) yielded no separation between *I. macrotis* and *I. zenkeri* apart from size differences (result not shown). The statement of Kingdon (1997: 179) that the tail of *I. macrotis* "is proportionately shorter" than that of *I. zenkeri* was not supported by the

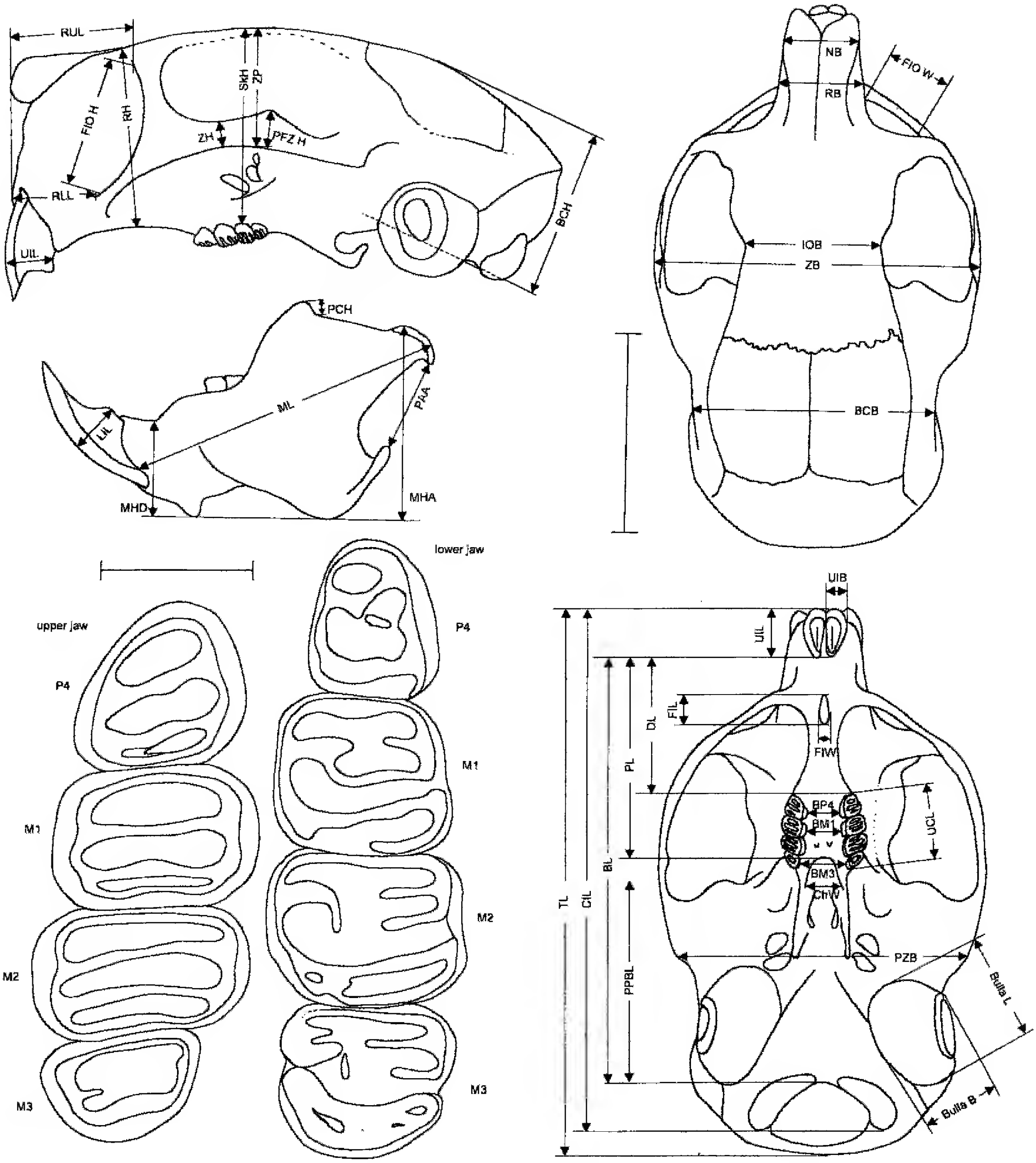


Fig. 1. Definition of linear measurements taken from skulls, as exemplified by a skull of *Idiurus macrotis* (ZMB 22885). Greatest length and width of single teeth (not marked in figure) were also taken. For abbreviations, see table 1. The scale for the dentition represents 1 mm and for the skull, 10 mm.

data used in our analysis (fig. 11). The tails of both species differ in absolute length (tables 6, 7), but the relative length is about the same.

When logarithmized absolute measurements of *I. macrotis* as well as residuals for hind-foot length were used for the PCA, then specimens from all areas strongly overlapped. *I. zenkeri* was not represented by sufficient geographic samples, so no conclusions were obtained for this species.

No weight data were available for any of the 80 specimens of *I. zenkeri* examined. Kingdon

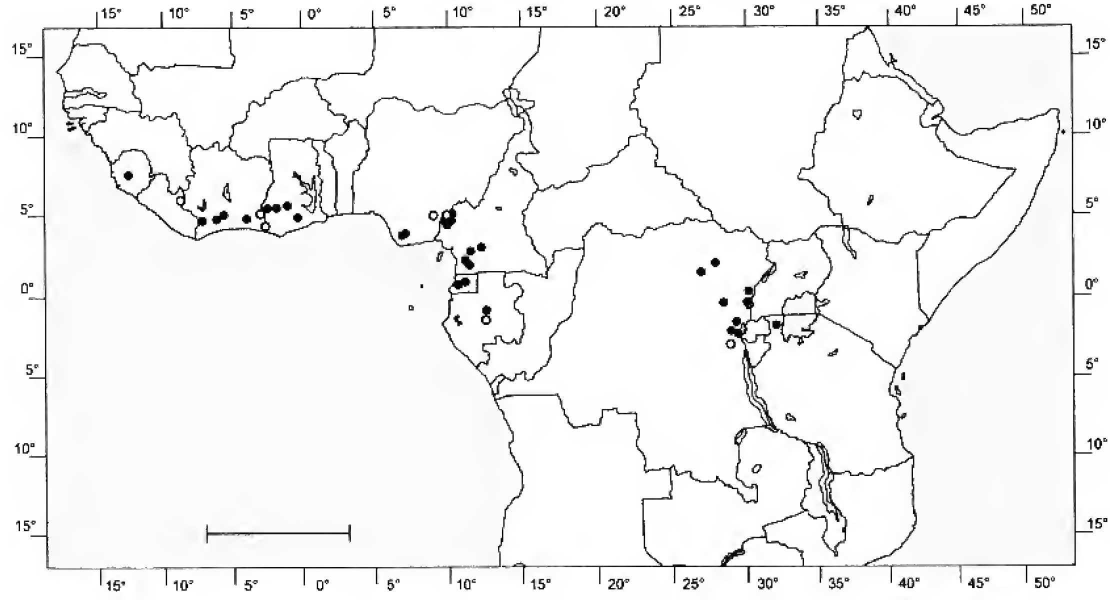


Fig. 2. Distribution of *I. macrotis* based on specimens examined and literature records. Closed symbols, specimens examined; open symbols, data taken from literature (Sanderson, 1940; Kuhn, 1965; Rahm, 1966; Adam, et al. 1970; Aellen et al., 1970; Julliot et al., 1998). Scale represents 1,000 km.

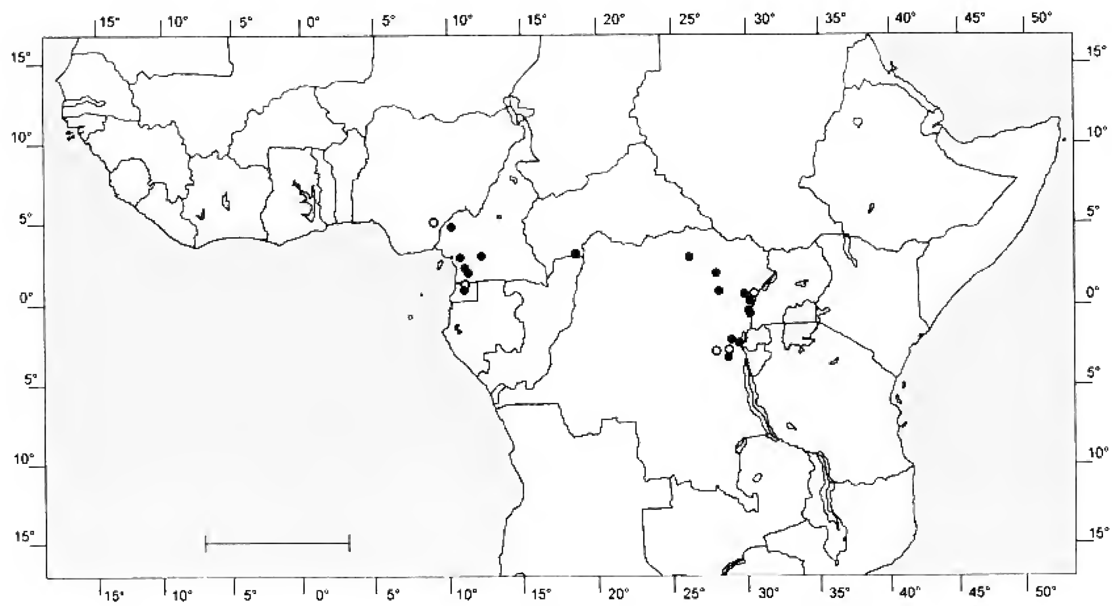


Fig. 3. Distribution of *I. zenkeri* based on specimens examined and literature records. Closed symbols, specimens examined; open symbols, data taken from literature (Rahm, 1966; Jones, 1971; Delany, 1975). Scale represents 1,000 km.

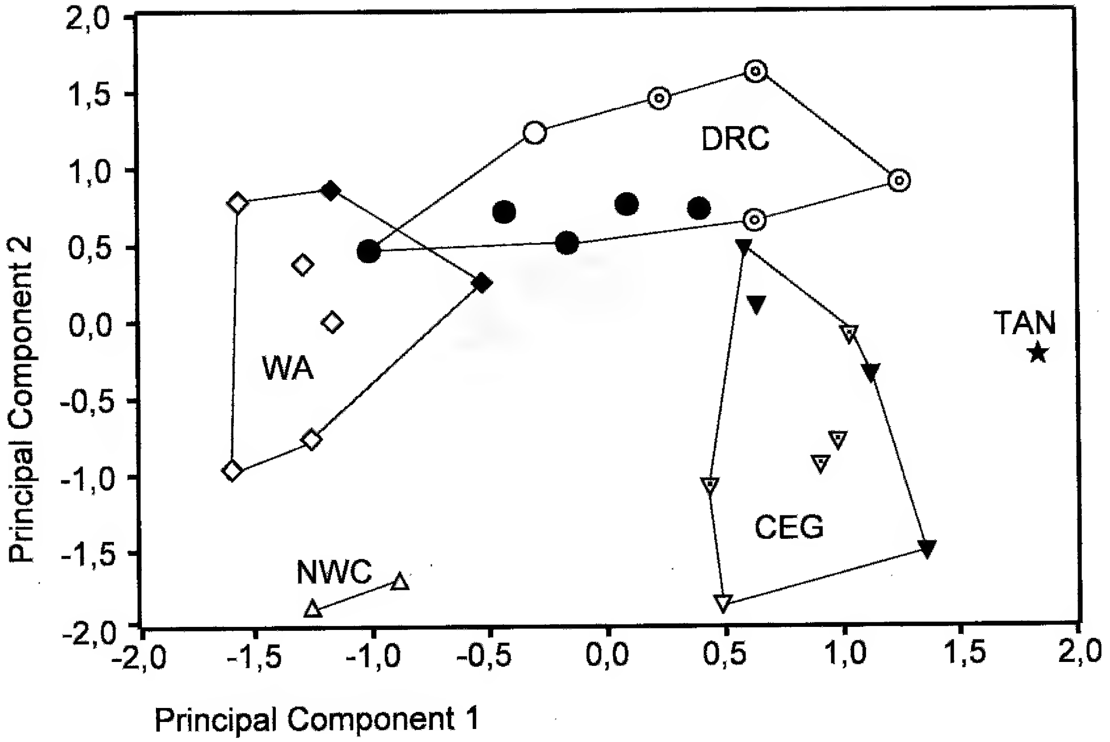


Fig. 4. Geographic variation of *I. macrotis* according to the first and second principal components as obtained from logarithmized absolute skull measurements. For characters, see table 1. Open symbols, males; closed symbols, females; symbols with a central dot, sex unknown; diamonds, West Africa; upright triangles, northwestern Cameroon; triangles pointing upside down, southern Cameroon to Gabon; circles, Democratic Republic of Congo; star, Tanzania.

(1997) gives a range of 14–17.5 g for this species and a range of 25–35 g for *I. macrotis*. Weight data for 14 museum specimens of *I. macrotis* (table 6) range from 23 g to 40 g.

The coloration of the studied skins appeared very similar in both species, in contrast to other anomalurid species (Schunke and Hutterer, 2005). In both species, the dorsal fur is grayish brown to dark brown, and the ventral fur is slightly paler. The skin of the limbs and the tail is lighter colored than the dorsal fur. *I. macrotis* specimens from Ghana seem to be lighter and more yellowish, but individuals from Ivory Coast are darker and more brownish, as are most specimens from Cameroon and the Congo. In *I. zenkeri* no differences could be found between populations, except for the holotype of *I. zenkeri*, which has an entirely blackish skin and dark brown fur.

## DISCUSSION

The taxonomic history of the genus *Idiurus* is brief. Matschie (1894) described the genus and species *Idiurus zenkeri* based on a single specimen from southern Cameroon (fig. 5). Subsequently, Miller (1898) named *I. macrotis* from the same region based on differences in size and coloration ("Much larger than *Idiurus zenkeri* Matschie; tail and ears relatively longer; color apparently darker; skull larger; bony palate narrower; second lower molar distinctly larger than first"). Lönnberg (1917) named *Idiurus zenkeri kivuensis* from Congo ("These specimens agree much more in their general characteristics with *Idiurus zenkeri* Matschie than with *I. macrotis* Miller. Especially the cranial dimensions differ from those of *I. macrotis*"). The taxon was subsequently given species status by Hayman

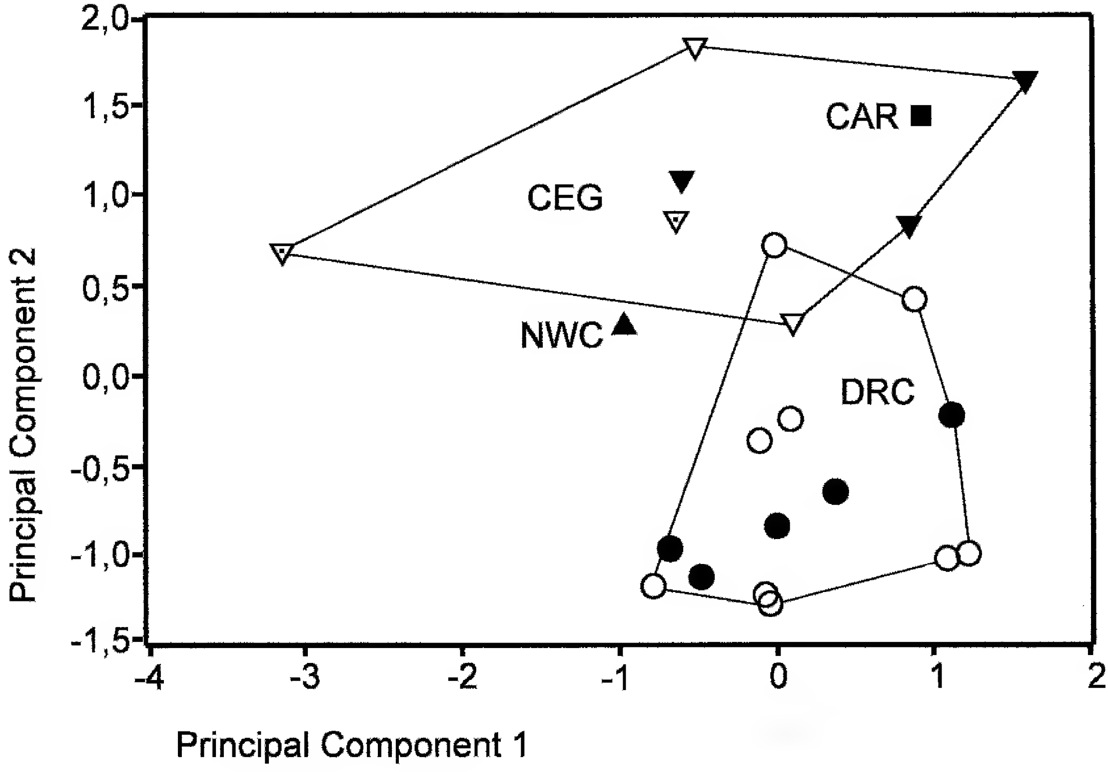


Fig. 5. Variation of *I. zenkeri* according to the first and second principal components as obtained from the logarithmized absolute skull measurements. For characters, see table 1. Open symbols, males; closed symbols, females; symbols with a central dot, sex unknown; upright triangles, northwestern Cameroon; triangles pointing upside down, southern Cameroon and Equatorial Guinea; square, Central African Republic; circles, Democratic Republic of Congo.

(1946) or considered a synonym of *I. zenkeri* (Verheyen, 1963), while Dieterlen (1993) listed it under *I. macrotis*, a conclusion that we share. A second, much smaller specimen reported by Lönnberg was considered a juvenile but may well be a specimen of *I. zenkeri*. Unfortunately the skull of the holotype of *kivuensis* is lost (Verheyen, 1963), and the skull of the smaller specimen is still inside the skin and not accessible. However, the general size of the holotype and the single skull measurement provided by Lönnberg (1917) led us to the conclusion that *kivuensis* is rather a synonym of *macrotis* than of *zenkeri*. Allen (1922) described *I. langi* and *I. panga* as new species from the northeastern Democratic Republic of Congo. *I. langi* was diagnosed as "[s]ize of and proportions nearly as in *Idiurus macrotis* Miller, but very different in coloration", and *I. panga* as "[s]imilar to *Idiurus macrotis* Miller, but much smaller and considerably paler throughout, including the basal fur". Hayman (1946), in a review of the genus, accepted *I. macrotis* and *I. zenkeri* as species, but also considered *I. kivuensis* a species ("In my view the conclusion must be drawn that there are only three species of *Idiurus*, namely *zenkeri, macrotis* and a species intermediate in size between these two, for which the name *kivuensis* is available"). He also named a new subspecies *I. kivuensis cansdalei* ("Differing from *I. k. kivuensis* in the pale general color above and below, and from *I. k. panga* in the general color of the hair tips above being between avellaneous and wood brown of Ridgway instead of light drab"). Finally, Verheyen (1963) named *Idiurus zenkeri haymani* from northwestern Cameroon: "Cette nouvelle sous-espèce se distingue de la forme typique par la longueur totale du corps, la longeur de l'oreille, la plus grande longeur du crâne et par la largeur bizygomatique nette-

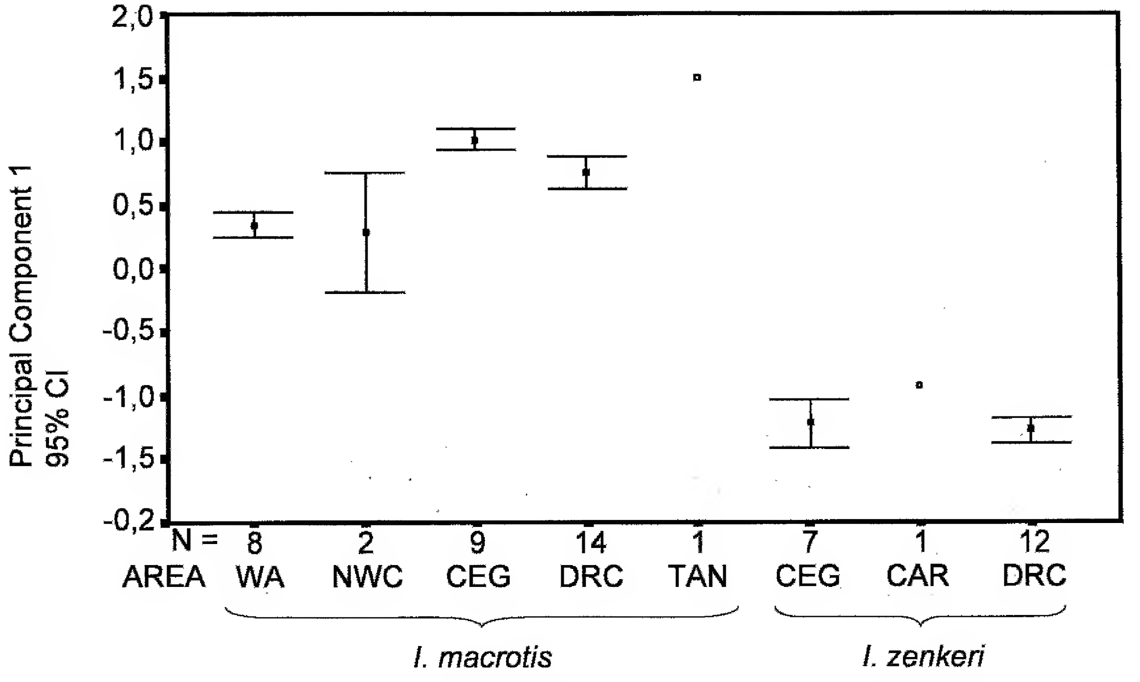


Fig. 6. Size variation of *I. macrotis* and *I. zenkeri* from the first principal component as obtained from logarithmized absolute skull measurements. For characters, see table 1.

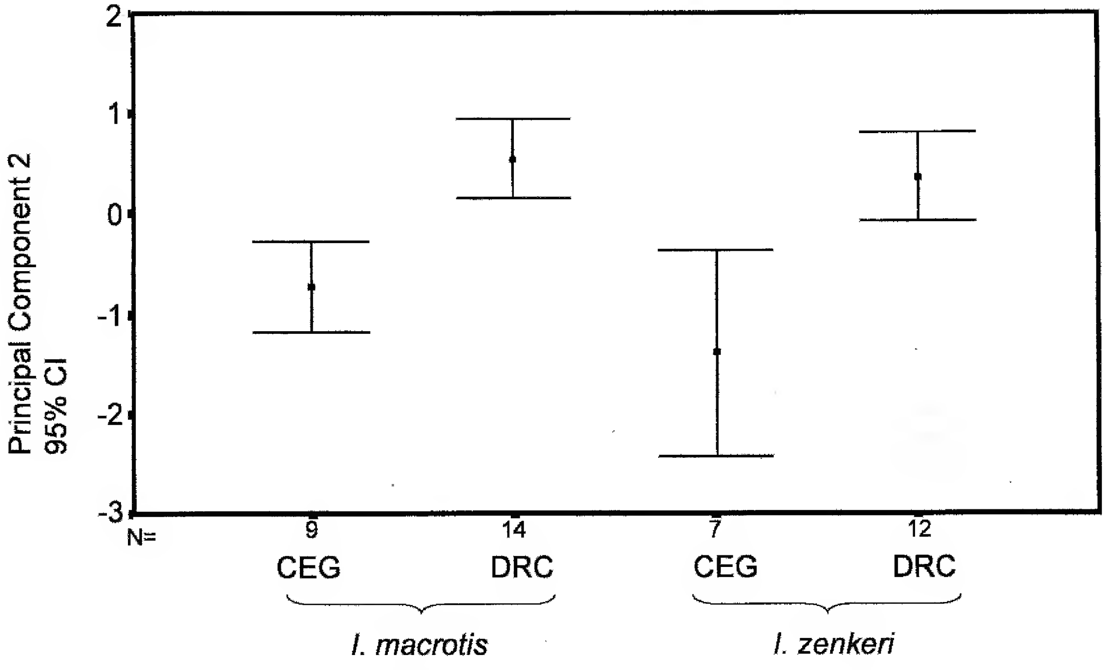


Fig. 7. Shape variation of *I. macrotis* and *I. zenkeri* from the second principal component as obtained from residuals calculated for palatilar length. For characters, see table 1.

TABLE 2

**Classification Results for *I. macrotis* (see text for details)**

Percentage of "grouped" cases correctly classified: 94.23%.

| | | Predicted group membership | | | |
|---|---|---|---|---|---|
| Actual group | N | WA | NWC | CEG | DRC |
| WA | 11 | 11<br>100.0% | 0<br>0.0% | 0<br>0.0% | 0<br>0.0% |
| NWC | 5 | 0<br>0.0% | 5<br>100.0% | 0<br>0.0% | 0<br>0.0% |
| CEG | 15 | 0<br>0.0% | 0<br>0.0% | 14<br>93.3% | 1<br>6.7% |
| DRC | 21 | 2<br>9.5% | 0<br>0.0% | 0<br>0.0% | 19<br>90.5% |

TABLE 3

**Classification Results for *I. zenkeri* (see text for details)**

Percentage of "grouped" cases correctly classified: 94.87%.

| | | Predicted group membership | |
|---|---|---|---|
| Actual group | N | NWC | DRC |
| NWC | 10 | 8<br>80.0% | 2<br>20.0% |
| DRC | 29 | 0<br>0.0% | 29<br>100.0% |

ment plus petites. … Il n'y pas de différence notable avec *Id. zenkeri zenkeri* quant aux caractères craniologiques et odontologiques ou de coloration du pelage". Although most current authors, like Dieterlen (1993), accept only two species, the seven available taxon names indicate that some underlying genetic variability may exist.

Our analysis principally supports the current concept of the two species *I. macrotis* and *I. zenkeri*. Both species are mainly separated by size but occur sympatrically in at least two different areas west and east of the Congo Basin (figs. 2–3) without intermediate forms.

Still, the results of the principal component analysis indicate the existence of morphologically distinguishable populations in *I. macrotis*, as we predicted from the patchy distribution of the species (fig. 2). Remarkable is the result that northwestern Cameroon and southern Cameroon to Gabon seem to have clearly different populations each (fig. 4). The former population matches the West African population in size but in shape is closer to specimens from southern Cameroon to Gabon. Animals

TABLE 4

**Mean Values and Ranges of Standard Skull Measurements in *I. macrotis***

| Area | Sex | N | TL | ZB | IOB | RH | UCL |
|---|---|---|---|---|---|---|---|
| WA | m | 9 | 25.3 (24.7–26.2) | 14.1 (13.7–14.6) | 6.0 (5.4–6.3) | 7.6 (7.4–7.7) | 3.3 (3.1–3.5) |
| | f | 4 | 25.7 (24.7–26.3) | 14.5 (14.4–14.6) | 6.2 (5.9–6.5) | 7.9 (7.8–8.0) | 3.4 (3.3–3.6) |
| NWC | m | 3 | 25.2 (24.4–25.9) | 14.1 (13.9–14.2) | 6.2 (6.0–6.4) | 7.7 (7.7–7.8) | 3.4 (3.3–3.6) |
| | f | 3 | 25.7 (25.7–25.8) | 14.2 (—) | 5.5 (5.4–5.7) | 7.6 (7.5–7.7) | 3.3 (3.2–3.4) |
| CEG | m | 5 | 27.2 (26.2–28.3) | 15.6 (15.3–15.8) | 6.3 (5.9–6.6) | 8.7 (8.4–9.0) | 3.7 (3.6–3.9) |
| | f | 5 | 27.8 (27.2–28.6) | 15.8 (15.3–16.3) | 6.4 (6.1–6.7) | 8.9 (8.3–9.5) | 3.7 (3.6–3.7) |
| DRC | m | 11 | 25.8 (25.2–26.4) | 15.3 (14.8–16.1) | 6.3 (5.6–6.7) | 8.3 (7.8–8.6) | 3.5 (3.4–3.7) |
| | f | 8 | 26.6 (25.6–27.3) | 15.4 (14.9–16.1) | 6.5 (6.1–6.7) | 8.4 (7.7–8.8) | 3.4 (3.3–3.7) |
| TAN | m | 1 | 28.1 (—) | 16.3 (—) | 6.3 (—) | 9.2 (—) | 3.7 (—) |

TABLE 5
**Mean Values and Ranges of Standard Skull Measurements in *I. zenkeri***

| Area | Sex | N | TL | ZB | IOB | RH | UCL |
|---|---|---|---|---|---|---|---|
| NWC | f | 2 | 19.7 (19.5–20.0) | *ca* 11.4 (—) | 5.3 (5.2–5.3) | 6.1 (5.9–6.2) | 2.3 (2.3–2.3) |
| CEG | m | 3 | 21.0 (20.3–21.6) | 12.2 (11.9–12.4) | 5.4 (5.2–5.5) | 6.5 (6.4–6.5) | 2.4 (2.3–2.5) |
| | f | 4 | 21.4 (20.9–22.2) | 12.3 (12.0–12.6) | 5.6 (5.4–5.8) | 6.6 (6.5–6.8) | 2.5 (2.4–2.5) |
| CAR | f | 1 | 22.6 (—) | 12.4 (—) | 5.5 (—) | 6.6 (—) | 2.5 (—) |
| DRC | m | 17 | 20.7 (20.2–21.3) | 12.3 (11.7–12.7) | 5.6 (5.2–6.1) | 6.4 (6.3–6.8) | 2.5 (2.4–2.7) |
| | f | 15 | 20.8 (20.8–21.6) | 12.4 (12.0–13.0) | 5.5 (5.2–5.7) | 6.5 (6.3–6.7) | 2.5 (2.3–2.7) |

TABLE 6
**Mean Values and Ranges of Standard Body Measurements of *Idiurus macrotis***
(total length partially calculated from head and body plus tail length)

| Area | Sex | N | Total L (mm) | Tail L (mm) | Hind foot (mm) | Ear (mm) | Weight (g) |
|---|---|---|---|---|---|---|---|
| WA | m | 5 | 219 (208–231) | 123 (117–130) | 21 (19–22) | 17 (16–18) | 25 (23–27) |
| | f | 5 | 218 (216–224) | 131 (124–140) | 21 (20–22) | 17 (16–18) | 33 (26–40) |
| NWC | m | 2 | 209 (201–217) | 119 (112–125) | 19 (18–20) | 16 (15–16) | — |
| | f | 5 | 207 (195–213) | 118 (105–129) | 18 (15.5–20) | 15 (14–16) | — |
| CEG | m | 3 | 230 (228–232) | 121 (120–122) | 20 (19–20) | 17 (16–18) | — |
| | f | 4 | 233 (200–254) | 126 (104–140) | 21 (20–23) | 17 (13–18) | 38 (37–39) |
| DRC | m | 4 | 217 (204–224) | 127 (117–133) | 21 (18–22) | 16 (14–18) | — |
| | f | 8 | 206 (199–212) | 123 (116–128) | 21 (21–21) | 17 (17–18) | — |

from the Democratic Republic of Congo differ mainly in size from the West African and northwestern Cameroon populations but differ in shape from the southern Cameroon to Gabon population. Differences are largest between specimens from northwestern Cameroon and from the Democratic Republic of Congo, on one hand, and specimens from southern Cameroon to Gabon and West Africa, on the other hand. This pattern does not suggest a clinal variation. A single individual from northwestern Tanzania (NMW 31089, fig. 9) has a very long and wide skull but is matched by a few other specimens. In the PCA, the specimen is closest to animals from southern Cameroon to Gabon in size and, particularly, in shape.

*I. macrotis* can thus be divided in five geographic populations: West Africa, northwestern Cameroon, southern Cameroon to

TABLE 7
**Mean Values and Ranges of Standard Body Measurements of *Idiurus zenkeri***
(total length partially calculated from head and body plus tail length)

| Area | Sex | N | Total L (mm) | Tail L (mm) | Hindfoot (mm) | Ear (mm) |
|---|---|---|---|---|---|---|
| NWC | f | 1 | 162 (—) | 91 (—) | 16 (—) | 9 (—) |
| CEG | m | 1 | 160 (—) | 75 (—) | 15 (—) | 14 (—) |
| | f | 1 | 185 (—) | — | 15 (—) | 13 (—) |
| CAR | f | 1 | 175 (—) | 105 (—) | 16 (—) | 12 (—) |
| DRC | m | 3 | 168 (157–175) | 97 (86–105) | 16 (15–18) | 14 (12–14) |
| | f | 4 | 173 (160–187) | 101 (97–108) | 17 (16–19) | 13 (12–14) |

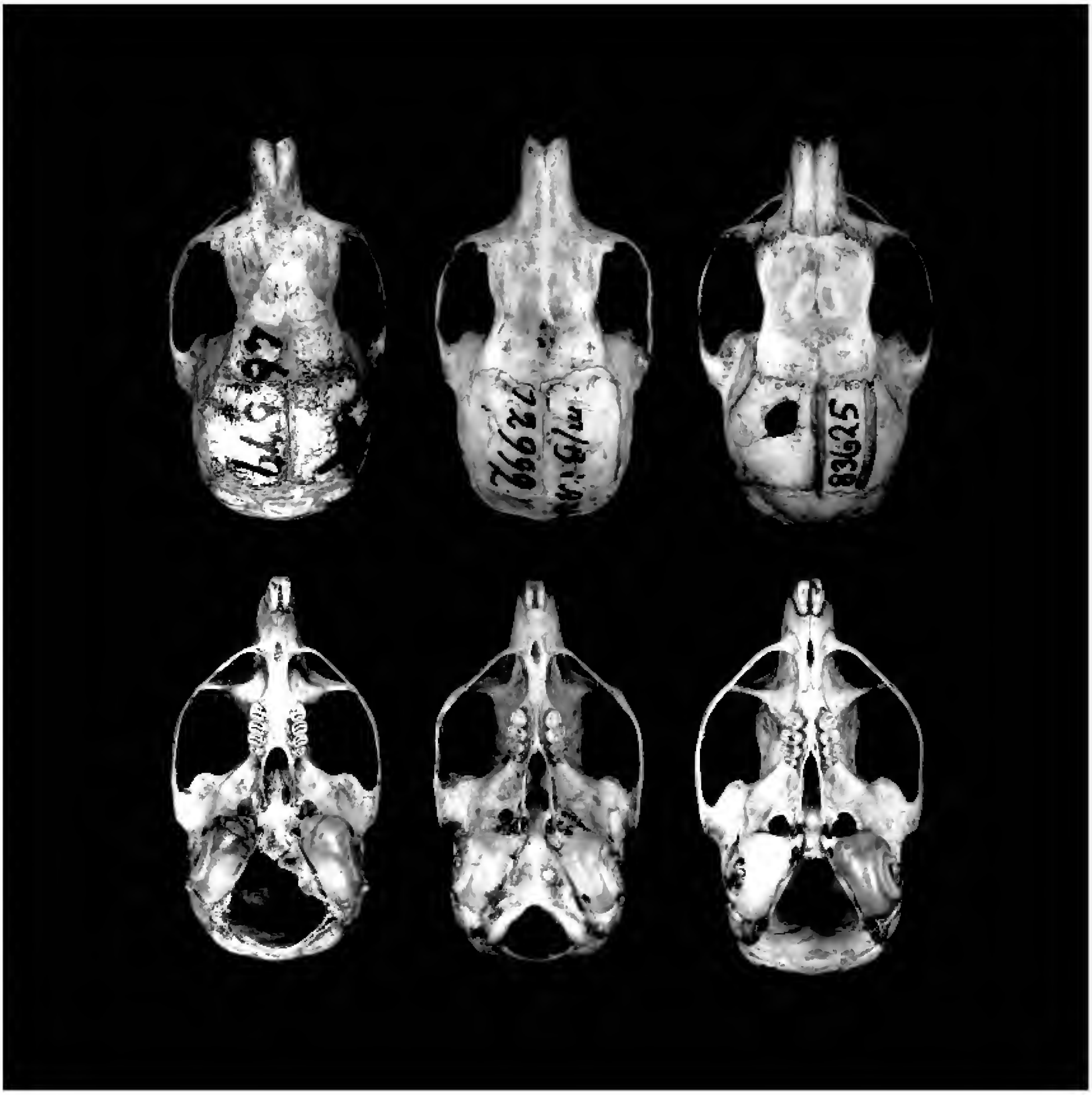

Fig. 8. Dorsal and ventral views of crania of *Idiurus macrotis*. From left to right: Oda, Ghana (BMNH 46.579, holotype of *cansdalei* Hayman, 1946); Ossidinge, northwestern Cameroon (ZMB 12992); Efulen, southern Cameroon (NMNH 83625, holotype of *macrotis* Miller, 1898).

Gabon, northeastern Democratic Republic of Congo, and Tanzania, by skull size and shape (figs. 4, 8–9). The cranial differences are not matched, however, by differences in body size (table 6) or coloration.

Results for *I. zenkeri* show a higher overlap between populations from Cameroon and the Democratic Republic of Congo. Specimens from northwestern Cameroon are less well separated than in *I. macrotis* (fig. 5). Still, the populations can be separated with the PCA, and individuals are likely to be classified correctly with a discriminant analysis (table 3). However, a clinal variation can not be excluded in this species, due to the intermediate position of animals from the Central African Republic. Further specimens, however, are necessary to test our results.

A subdivision as in *I. macrotis*, though more provisional, is possible in *I. zenkeri*. Animals

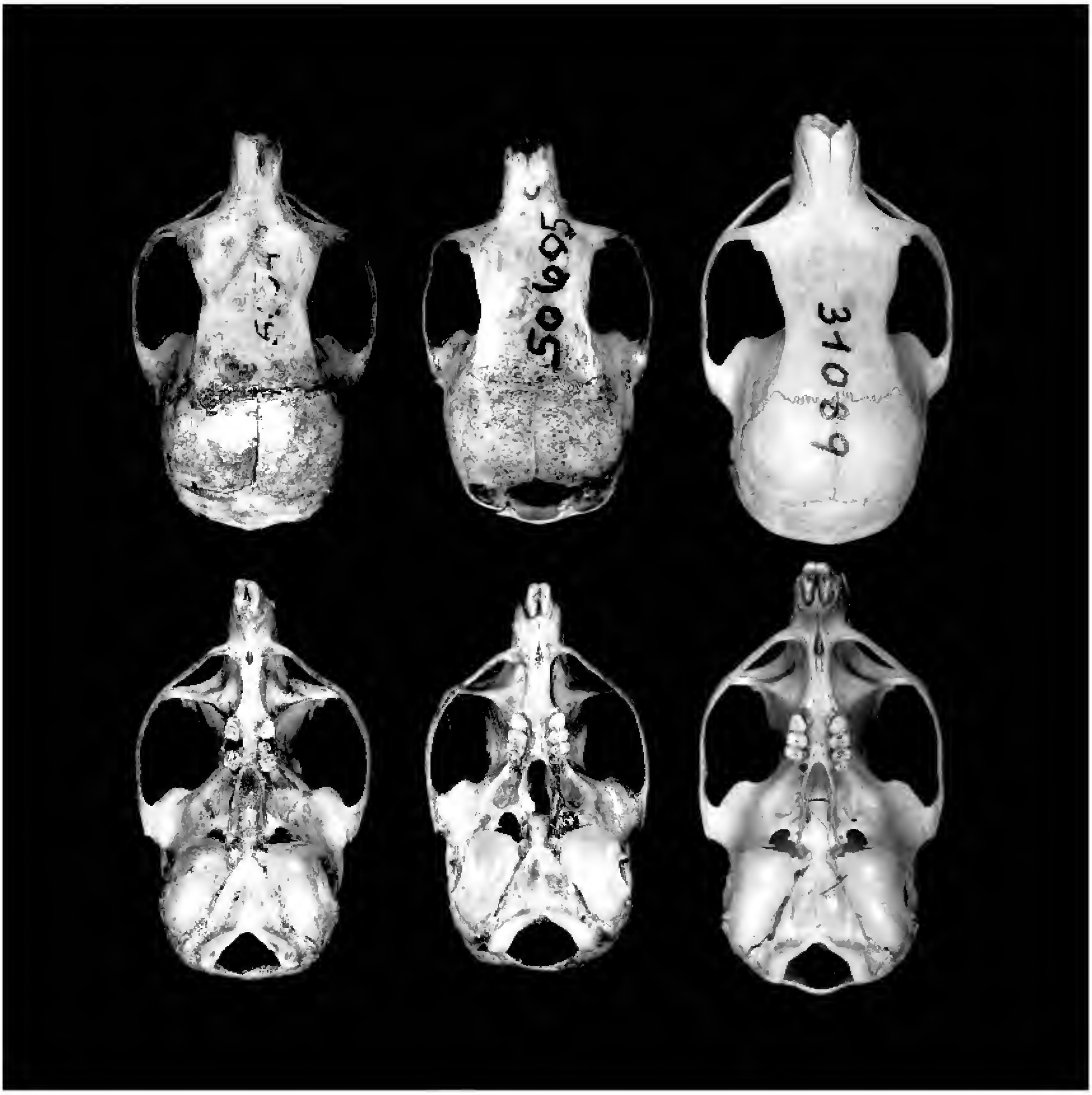


Fig. 9. Dorsal and ventral views of crania of *Idiurus macrotis*. From left to right: Medje, Democratic Republic of Congo (AMNH 50542, holotype of *langi* Allen, 1922); Panga, DRC (AMNH 50605, holotype of *panga* Allen, 1922); northwestern Lake Victoria, Tanzania (NMW 31089).

from southern Cameroon plus Equatorial Guinea and the northeastern Democratic Republic of Congo can be recognized, and less so animals from northwestern Cameroon (figs. 5, 10). The position of animals from the Central African Republic remains unsettled until further specimens become available. As in *I. macrotis*, body measurements and coloration provide no clue to geographical variation.

The case of the enigmatic holotype skin of *I. zenkeri* (fig. 12) requires some explanation. In the series of 80 fairly uniform skins that we examined, the holotype is the only case where the fleshy parts of the skin have an equally blackish color. The skull (fig. 10), however, groups nicely with other specimens from southern Cameroon and Equatorial Guinea (fig. 5). We assume that the blackish coloration of the type skin in the Berlin Museum is

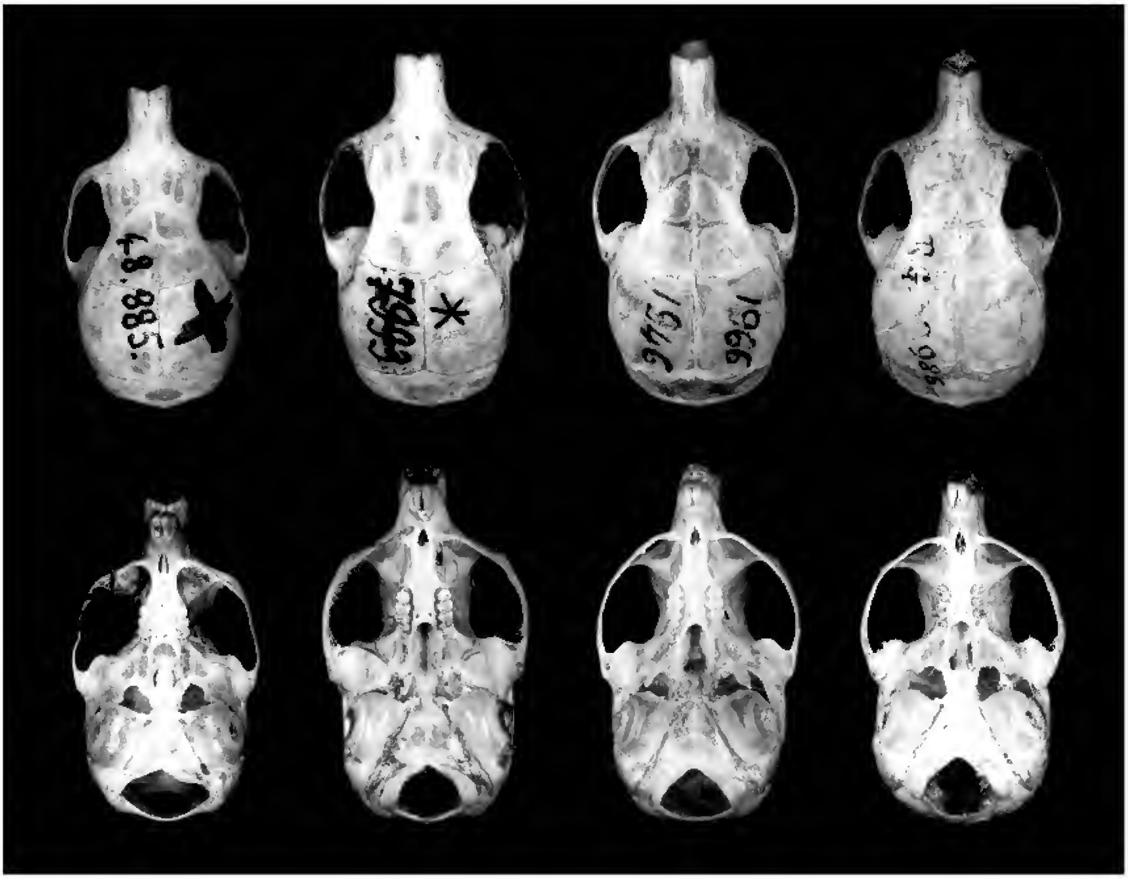

Fig. 10. Dorsal and ventral views of crania of *Idiurus zenkeri*. From left to right: Eshobi, northwestern Cameroon (BMNH 48.885, holotype of *haymani* Verheyen, 1963); Yaoundé, southern Cameroon (ZMB 7993, holotype of *zenkeri* Matschie, 1894); La Maboké, Central African Republic (MNHN 1966-1946); Kashewe, Democratic Republic of Congo (MRAC 30986).

an artifact. A similar case, also related to the Berlin Museum, is a mouse described by Dieterlen (1986) as *Togomys melanoderma* from older African collections and diagnosed as having "all unhaired parts of the skin deep black". A subsequent inspection (Dieterlen, 1989) of the animal revealed its identity with Asian *Rattus exulans* but with the skin stained black by some unknown chemical process.

Another interesting aspect of our study is the shape difference between populations from southern Cameroon to Gabon and the Democratic Republic of Congo for both *I. macrotis* and *I. zenkeri*. Specimens were separated by the second principal component according to their geographic origin rather than according to species (fig. 7). The factor had particularly high loadings for bulla size and rostrum length. Animals from Cameroon tended to have a longer rostrum, larger incisors, and smaller bullae, independent of species status. This finding may reflect unknown parallel adaptations in both species, for which we lack any supportive biological data.

## CONCLUSIONS

Both species of *Idiurus* show a very uniform coloration throughout their range. Although some skins of *I. macrotis* from Ghana were slightly paler, no differences in skull size or shape between specimens from Ghana and other West African populations could be detected.

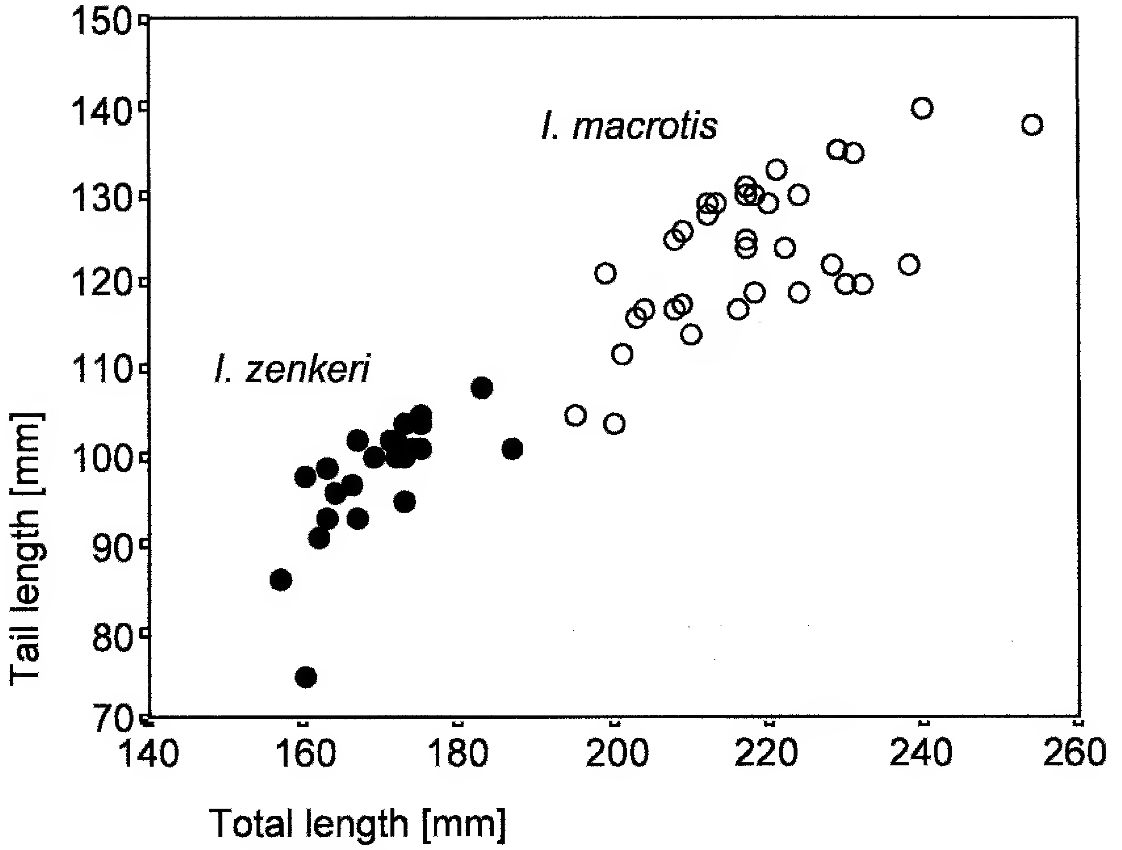


Fig. 11. Bivariate plot of tail length versus total length in *Idiurus macrotis* ($N$ = 34) and *I. zenkeri* ($N$ = 22). All geographic samples combined.

Our morphometric study has revealed some differences in both species at the population level, but we feel that a translation of these differences into named subspecies is not warranted at this moment. Size and shape differences do not follow clear patterns. For *I. macrotis*, size would produce clusters with specimens from West Africa, northwestern Cameroon, and, perhaps, southern Cameroon to Gabon and Tanzania. Individuals from Congo show intermediate values and overlap with the two main groups. If shape differences are taken, then the populations from southern Cameroon to Gabon are similar to West Africa and northwestern Cameroon, but different from the Congo sample. Only combined data distinguish between allopatric populations.

Populations of *I. zenkeri* from southern Cameroon (and Equatorial Guinea) and the Democratic Republic of Congo overlap, and the intermediate position of some specimens from Central African Republic suggest a clinal variation. Individuals from northwestern Cameroon are slightly smaller than those of other populations, but there are no differences in shape.

In summary, it is possible to distinguish between geographic populations of the two species, but neither size nor shape provides clear patterns. If one were to accept size differences as sufficient for a taxonomic division in one case, shape differences would have to be ignored, and vice versa.

Many of the specimens that we studied were collected almost a century ago. The specimens of both species obtained in 1910 by the American Museum Congo Expedition (Allen, 1922) still belong to the best series available for systematic studies. The unique specimen

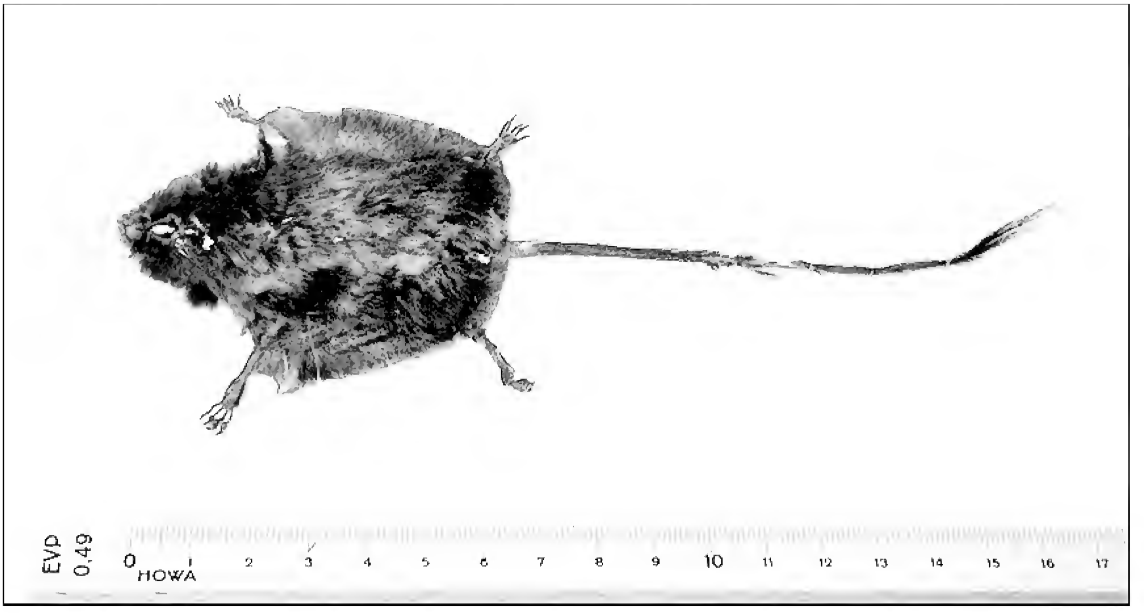


Fig. 12. Study skin of the holotype of *Idiurus zenkeri* (ZMB 7993) showing the dark staining of the fleshy parts of the skin and the fur.

from Tanzania (fig. 9) was collected by Rudolf Grauer in 1905 in one of the forest islands in the northwest of Lake Victoria (K. Bauer, personal commun.). It is unknown whether this forest and its *Idiurus* population still exist.

With such limited information available, we cannot decide whether the clusters in both species, for which we found evidence, represent populations or perhaps cryptic species. Future chromosome and genetic studies may shed further light on this widely unknown group of forest gliders. For the moment, we suggest the following taxonomic arrangement:

### *Idiurus macrotis* Miller

*Idiurus macrotis* Miller, 1898, p. 73; holotype: NMNH 83625; type locality: "Efulen, Cameroons".

*Idiurus kivuensis cansdalei* Hayman, 1946, p. 211; holotype: BMNH 46.579; type locality: "Oda, Oda Province, Ghana".

*Idiurus zenkeri kivuensis* Lönnberg, 1917, p. 67; holotype: NRM not cataloged; type locality: "Masisi, Kivu district, Congo Belge".

*Idiurus langi* Allen, 1922, p. 69; holotype: AMNH 50542; type locality: "Medje, Belgian Congo".

*Idiurus panga* Allen, 1922, p. 70; holotype: AMNH 50605; type locality: "Panga, Belgian Congo".

### *Idiurus zenkeri* Matschie

*Idiurus zenkeri* Matschie, 1894, p. 197; holotype: ZMB 7993; type locality: "Yaunde, Cameroons".

*Idiurus zenkeri haymani* Verheyen, 1963, p. 181; holotype: BMNH 48.885; type locality: "Eshobi bush, Mamfe District, Nigérie, 550 ft".

## ACKNOWLEDGMENTS

We are grateful to the curators and staff members who shared their time to support our studies during visits and with loans. We particularly thank Bob Randall (AMNH); Paula D. Jenkins (BMNH); Bruce D. Patterson (FMNH); Jacques Cuisin, Michel Tranier, and Jean-François Dubois (MNHN); Wim Van Neer and Wim Wendelen (MRAC); Urs Rahm (NHMB); Yakub M. Dahiye (NMK); Helen Kafka, Linda Gordon, and Richard Thorington (NMNH); Barbara Herzig (NMW); Olavi Grönwall (NRM); Chris Smeenk (RMNH); Dieter Kock (SMF); Fritz Dieterlen (SMNS); and Manfred Ade, Robert Asher, Irene Thomas, and Detlef Willborn (ZMB). We thank David Tarkhnishvili for his help with the statistical analyses; he and Meredith Happold, Gustav Peters, and

Bradley Sinclair read and improved drafts of the manuscript. Hendrik Turni and Uwe Vaartjes assisted in the preparation of the photographs and figures. Financial support was provided by the Deutsche Forschungsgemeinschaft (DFG, HU 430/1-1). Visits to the BMNH and the MNHN were funded by the TMR Programme of the European Commission (Bioresource London and Parsyst Paris).

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# APPENDIX 1

## Localities and Specimens Examined

Localities of specimens that were not examined in this study but are known from literature are marked by an asterisk.

*Idiurus macrotis*

**SIERRA LEONE**: Kasewe (= Kassewe), 8°19′N 12°11′W (BMNH 62.1839). **LIBERIA**: Deaple* (= Diaple), 6°51′N 8°24′W. IVORY COAST: Bianou* (= Bianouan), 6°00′N 3°11′W; Bouroukrou, 5°51′N 4°11′W (MNHN 1908-61); Ehania*, 5°13′N 2°46′W; Grabazouo (= Grabagoua, Grabazzo), 5°41′N 6°13′W (MNHN 1985-220); Lakota ("15 km N. Lakota [Guéboua]"), 6°00′N 5°43′W (AMNH 239578, 239579, 241151, 241152); Mt. Nimba, Grassfield (NMK 538, 539, 540); Tai National Park, ca. 5°40′N 7°06′W (SMF 89949, 89950). **GHANA**: Ahiriso, 6°32′N 2°20′W (NMNH 414453); Kumasi, 6°41′N 1°37′W (BMNH 65.770); Mafia (= Sifuri-Mafia), 6°26′N 2°56′W (MRAC 38519, 38520); Oda, 5°54′N 0°59′W (BMNH 46.407, 46.408, 46.579 holotype *cansdalei*, 46.580, 46.581, 46.582, FMNH 62787). **NIGERIA**: Igovia, 4°58′N 6°29′E (BMNH 1996.313); Okaka, East of Yenagoa [4°55′N, 6°15′E] (BMNH 1996.566, 1996.567). **CAMEROON**: Atolo*, 6°11′N 9°27′E; Bashauo*, 6°08′N 8°25′E; Besongabang (= Beshongaba, Besong Abang, Besang Abang), 5°44′N 9°16′E (BMNH 48.874, 48.875); Bipindi, 3°06′N 10°30′E (ZMB 11689, 11690, 15304, 22744, 22745, 22746, 22748, 22752, 22753, 22754, 22758, 22759, 22760, 22763, 22765, 22766, 22877, 22885, 22886, 22887, RMNH 25766a, 25766b); Bipindi or Yaoundé (ZMB 10086, 10087, 10088); Efulen, 2°46′N 10°42′E (BMNH 3.2.4.14, 3.2.4.15, 3.2.4.16, 3.2.4.36, 3.2.4.37, 8.6.23.7, NMNH 83625 holotype *macrotis*, 83626); Esaka (= Eséka), 3°39′N 10°46′E (AMNH 236384); Eshobi (= Eshobe), 5°47′N 9°22′E (BMNH 48.871, 48.872, 48.873); Ossidinge, 5°55′N 9°05′E (ZMB 12992); Sinba, probably close to Tinta (BMNH 48.877); Tinta, 6°15′N 9°30′E (BMNH 48.876); Yaounde, 3°52′N 11°31′E (ZMB 13843). **EQUATORIAL GUINEA**: Near Benito R., 20 mi from mouth, 1°32′N 9°50′E (BMNH 99.4.6.11); Monte Alen, 1°40′N 10°17′E (MNHN 1999-463). **GABON**: Booué (= Booui), 0°5′S 11°56′E (MNHN 1949-49); La Makandé*, 0°40′S 11°54′E. **DEMOCRATIC REPUBLIC OF CONGO**: Angumu, 0°8′S 27°43′E (MRAC 14227); Biripange*, river close to Kisanga [Kankisi]; Irangi, 1°54′S 28°27′E (MRAC 28377, NHMB 7359, SMNS 43325); Kabingu*, close to Irangi (NHMB 7357); Kalehe (= Kashewe), 2°06′S 28°55′E (MRAC 30992, 30993); Kankisingi* (= Kisanga), 2°41′S 28°08′E; Keba*, close to Kisanga (Kankisi); Luhoho ("Irangi, vallée d. l. rivière Luhoho"), close to Irangi (MRAC 30996); Lwake, close to Irangi (MRAC 28375, 28376, 28378); Mabondo ("Irangi, colline Mabondo"), close to Irangi (MRAC 30994, 30995); Masisi, 1°23′S 28°48′E (NRM uncataloged holotype *kivuensis*); Medje, 2°23′N 27°18′E (AMNH 50531, 50532, 50533, 50536, 50542 holotype *langi*, MRAC 12401); Mitala*, close to Kisanga [Kankisi]; Tshoko*, close to Kisanga [Kankisi]; Oisha-Lusilube, 0°30′N 29°39′E (MRAC 82011M516, 82011M519, 82011M520, 82011M521, 82011M522, 82011M523, 82011M524, 82011M525); Panga, 1°50′N 26°22′E (AMNH 505604, 50605 holotype *panga*, 50606, 50607); Semliki, 0°8′S 29°36′E (MRAC 82011M517, 82011M518, 82011M526); Yeke, close to Irangi (NHMB 7356). **TANZANIA**: Lake Victoria, southwest of Lake Victoria (NMW 31089).

*Idiurus zenkeri*

**CAMEROON**: Bashauo*, 6°08′N 8°25′E; Bipindi, 3°06′N 10°30′E (RMNH 25765a, 25765b, ZMB 13844, 22743, 22747, 22749, 22750, 22755, 22756, 22762, 22764, 22767, 36375, 22747, 22751, 22757, 36374); Dipikar Island*, 2°12′N 10°30′E; Edéa, 3°47′N 10°07′E (ZMB 36327, 36328, 36329, 36330); Efulen, 2°46′N 10°42′E (BMNH 3.2.4.38, 8.6.23.8, NMNH 125438); Eshobi (= Eshobe), 5°47′N 9°22′E (BMNH 48.885 holotype *haymani*, 48.886); Yaoundé, 3°52′N 11°31′E (ZMB 7993 holotype *zenkeri*, ZMB 15303). **EQUATORIAL GUINEA**: Benito, 1°34′N 10°24′E (BMNH 98.10.7.11). **CENTRAL AFRICAN REPUBLIC**: Lamaboke (= La Maboké, Mbaiki), 3°52′N 17°59′E (MNHN 1966-1946, 1992-1214, 1992-1215). **DEMOCRATIC REPUBLIC OF CONGO**: Avakubi, 1°20′N 27°33′E (AMNH 50613); Bambesa, 3°27′N 25°42′E (MRAC 14683, 14684); Biripange*, riv. close to Kisanga [Kankisi]; Inangongo, probably close to Oisha-Lusilube (MRAC

82011M507); Irangi (NHMB 7360, 7361, 7362); Ituri River, 50 m. S. W. Irumu, 0°59′N 29°19′E (BMNH 30.11.11.267, 30.11.11.268, 30.11.11.269); Kabingu*, close to Irangi; Kalehe (= Kashewe), 2°06′S 28°55′E (MRAC 30985, 30986, 30987, 30988, 30989); Kamituga, 3°04′S 28°10′E (MRAC 31468); Kankisingi* (= Kisanga), 2°41′S 28°08′E; Keba*, close to Kisanga [Kankisi]; Mabondo ("Irangi, colline Mabondo"), close to Irangi (MRAC 30991); Makwe, close to Irangi (MRAC 29333, 29334); Mashere*, close to Irangi; Medje, 2°23′N 27°18′E (AMNH 50529, 50534, 50535, 50537, 50538, 50539, 50540, 50541, 50543, 50544, 50545, 50546, 50548, 50550, 50601, 50602, 50603, 50612, 50622, MRAC 12399, 12400); Mitala*, close to Kisanga [Kankisi]; Tshoko*, close to Kisanga [Kankisi]; Muhutaba ("Irangi, vallée d. l. rivière Muhutaba"), close to Irangi (MRAC 30990); Niamiringi*, West of Lake Kivu; Oisha-Lusilube, 0°30′N 29°39′E (MRAC 82011M508, 82011M509, 82011M510, 82011M511, 82011M512, 82011M513); Semliki, 0°8′S 29°36′E (MRAC 82011M514, 82011M515); Shabunda*, 2°41′S 27°20′E; Tshoko*, close to Irangi. **UGANDA**: Bwamba*, 0°48′N 30°06′E.

## APPENDIX 2

### Specimens Used for Morphometric Analyses

(m, male; f, female; a, skull measurements taken; b, body measurements taken)

*Idiurus macrotis*

**WA (WEST AFRICA)**: AMNH 239578 (m) a b; AMNH 239579 (m) a b; AMNH 241151 (m) a b; AMNH 241152 (f) b; BMNH 46.407. (m) a; BMNH 46.408. (m) a; BMNH 46.579 (m) a b; BMNH 46.580 (f) a b; BMNH 46.581 (m) b; BMNH 46.582 (m) a; BMNH 62.1839 (m) a; BMNH 65.770 (f) a; FMNH 62787 (f) b; MNHN 1908-61 (m) a; MNHN 1985-220 (f) a b; NMNH 414453 (f) a b; SMF 89949 (f) b; SMF 89950 (m) b. **NWC (NORTHWESTERN CAMEROON)**: BMNH 48.871 (m) a b; BMNH 48.872 (f) a b; BMNH 48.873 (f) a b; BMNH 48.874 (f) b; BMNH 48.875 (f) a b; BMNH 48.876 (m) a b; BMNH 48.877 (f) b; ZMB 12992 (m) a. **CEG (SOUTHERN CAMEROON, EQUATORIAL GUINEA, AND GABON)**: AMNH 236384 (f) a b; BMNH 3.2.4.14. (m) a b; BMNH 3.2.4.15. (m) b; BMNH 3.2.4.16. (f) a b; BMNH 3.2.4.36. a; BMNH 3.2.4.37. a; BMNH 8.6.23.7. (f) a b; BMNH 99.4.6.11. (m) a b; MNHN 1999-463 (f) a b; NMNH 83626 (m) a; NMNH 83625 (m) a; ZMB 13843 a; ZMB 10087 (f) a; ZMB 10088 (m) a; ZMB 22744 a; ZMB 22748 a; ZMB 22766 a; ZMB 22885 a. **DRC (DEMOCRATIC REPUBLIC OF CONGO)**: AMNH 50531 (m) a b; AMNH 50532 (m) a b; AMNH 50533 (m) a b; AMNH 50536 (m) a b; AMNH 50604 (f) a b; AMNH 50606 (f) a b; AMNH 50607 (m) a b; AMNH 50542 (m) a b; AMNH 50605 (f) a b; MRAC 14227 (m) a; MRAC 28375 (f) a; MRAC 28376 (f)? a; MRAC 28377 (m) a; MRAC 28378 (f) a; MRAC 30992 (f) a; MRAC 30993 (f) a; MRAC 30994 (m) a; MRAC 30995 (m) a; MRAC 30996 (f) a; MRAC 12401 (m) a; MRAC 82011M516 a; MRAC 82011M517 a; MRAC 82011M518 a; MRAC 82011M519 a; MRAC 82011M520 a; MRAC 82011M521 a; MRAC 82011M522 a; MRAC 82011M523 a; MRAC 82011M524 a; SMNS 43325 (f) b. **TAN (TANZANIA)**: NMW 31089 (m) a.

*Idiurus zenkeri*

**NWC (NORTHWESTERN CAMEROON)**: BMNH 48.885 (f) a; BMNH 48.886 (f) a b. **CEG (SOUTHERN CAMEROON AND EQUATORIAL GUINEA)**: BMNH 3.2.4.38. (m) a; BMNH 8.6.23.8. (m) a b; BMNH 98.10.7.11. (f) a; NMNH 125438 (f) a b; ZMB 22747 a; ZMB 22751 (m) a; ZMB 22757 (f) a; ZMB 36330 a; ZMB 7993 (f) a. **CAR (CENTRAL AFRICAN REPUBLIC)**: MNHN 1966-1946 (f) a b; MNHN 1992-1215 a. **DRC (DEMOCRATIC REPUBLIC OF CONGO)**: AMNH 50529 (m) a b; AMNH 50534 (f) a b; AMNH 50535 (f) a b; AMNH 50537 (f) a b; AMNH 50538 (f) a b; AMNH 50539 (m) a b; AMNH 50540 (m) a b; AMNH 50541 (f) a b; AMNH 50543 (m) a b; AMNH 50544 (m) a b; AMNH 50545 (f) a b; AMNH 50546 (m) a b; AMNH 50548 (m) a b; AMNH 50550 (m) a b; AMNH 50601 (f) a b; AMNH 50602 (m) a b; AMNH 50603 (m) a b; AMNH 50612 (f) a b; AMNH 50613 (f) a b; BMNH 30.11.11.267 (m) a b; BMNH 30.11.11.268 (m) a b; BMNH 30.11.11.269 (m) a b; MRAC 12399 (m) a; MRAC 12400 (f) a; MRAC 30985 (m) a; MRAC 30986 (m) a; MRAC 30987 (f) a; MRAC 30988 (f) a; MRAC 30989 (m) a; MRAC 30990 (f) a; MRAC 30991 (f) a; MRAC 31468 (f) a; MRAC 82011M508 a; MRAC 82011M509 a; MRAC 82011M510 a; MRAC 82011M512 a; MRAC 82011M513 a.

# APPENDIX 3

## Statistics for Principal Component and Discriminant Analyses

(tables 8–12)

TABLE 8
**Factor Matrix for *Idiurus macrotis***

Loadings given for first and second principal component and percentage of variation explained by the two axes; see fig. 4.

| | Factor 1 | Factor 2 |
|---|---|---|
| % Variation | 45.3 | 12.1 |
| BL | .89271 | −.03994 |
| RB | .57460 | −.44016 |
| IOB | .42287 | .05915 |
| BCB | .75799 | .47330 |
| PL | .88167 | −.07622 |
| FIB | −.12982 | −.01727 |
| BP4 | −.22887 | .76757 |
| BM1 | −.36340 | .36513 |
| ChB | −.07559 | −.20205 |
| Bulla L | .48480 | .71294 |
| Bulla B | .30567 | .53139 |
| RH | .92160 | −.00711 |
| PZB | .87564 | .26807 |
| FIOH | .91939 | .10029 |
| FIOB | .77912 | .07743 |
| RUL | .53595 | −.49951 |
| RLL | −.13780 | −.49637 |
| ML | .96589 | .05219 |
| MHA | .81578 | −.03721 |
| PAA | .16019 | −.55647 |
| PCH | .35456 | −.07658 |
| UIL | .85114 | −.02140 |
| UIB | .83208 | .00572 |
| LCL | .74536 | −.39142 |
| LIB | .81874 | .22361 |
| LIL | .90567 | −.22996 |

TABLE 9
**Factor Matrix for *Idiurus zenkeri***

Loadings given for first and second principal component and percentage of variation explained by the two axes; see fig. 5.

| | Factor 1 | Factor 2 |
|---|---|---|
| % Variation | 25.8 | 19.6 |
| IOB | .61104 | −.34238 |
| PL | .60475 | .09994 |
| FIL | .13913 | −.58238 |
| FIB | .43075 | .01658 |
| BP4 | .42466 | .23185 |
| BM1 | .40565 | .40217 |
| ChB | .46364 | −.47408 |
| Bulla L | .46778 | −.38472 |
| Bulla B | .55127 | −.57800 |
| RH | .89205 | .22853 |
| ZP | .00498 | −.23157 |
| PZB | .84112 | .24663 |
| FIOH | .61711 | .55274 |
| FIOB | .44249 | −.24439 |
| RUL | −.00953 | .76349 |
| RLL | −.07509 | .74154 |
| ML | .82464 | −.08345 |
| MHA | .74172 | .20935 |
| PCH | −.01708 | .12574 |
| UIL | .25698 | .68782 |
| UIB | −.39812 | .58112 |
| LIL | .46616 | .56528 |
| LIB | −.38926 | .49820 |

TABLE 10
**Factor Matrix for *Idiurus macrotis* and *I. zenkeri***

Loadings given for first and second principal component and percentage of variation explained by the two axes; see figs. 6 and 7. Left: Size-In function, with ln-transformed measurements; only factor 1 was used in fig. 6. Right: Size-Out function, residuals for palatilar length; only factor 2 used in fig. 7.

| | Size-In | | Size-Out | |
|---|---|---|---|---|
| | Factor 1 | Factor 2 | Factor 1 | Factor 2 |
| % Variation | 67.6 | 8.4 | 23.2 | 17.0 |
| BL | .98804 | −.02322 | .70601 | .05812 |
| IOB | .88048 | −.00040 | .37676 | −.26112 |
| PL | .98318 | −.04043 | — | — |
| FIB | .29735 | .65606 | .31079 | −.02096 |
| BP4 | −.10572 | .78203 | .33529 | −.36381 |
| BM1 | .11286 | .79020 | .50475 | −.00386 |
| ChB | .40335 | .32405 | .27156 | .01277 |
| Bulla L | .95096 | .01003 | .09345 | −.70948 |
| Bulla B | .87914 | .08560 | .26589 | −.70060 |
| RH | .97993 | −.04984 | .80326 | .06252 |
| PZB | .98693 | .03677 | .85911 | −.07708 |
| FIOH | .97779 | −.03977 | .76461 | .09471 |
| FIOB | .88895 | −.04122 | .25728 | −.33498 |
| RUL | .88913 | −.08352 | .30881 | .73400 |
| RLL | .38931 | .11776 | −.00619 | .66149 |
| ML | .98769 | −.03132 | .66413 | −.25691 |
| MHA | .97851 | −.03595 | .56069 | −.13428 |
| PCH | .55525 | .11394 | .27676 | .07851 |
| UIL | .96659 | .01739 | .55553 | .59190 |
| UIB | .83488 | −.08089 | −.21055 | .54083 |
| LIL | .97771 | −.09518 | .51417 | .63444 |
| LIB | .87079 | −.10438 | −.20289 | .35919 |

TABLE 11
**Standardized Canonical Discriminant Function Coefficients for *Idiurus macrotis***

Loadings given for first three canonical axes and percentage of variation explained by the three axes; see table 2.

| | Function 1 | Function 2 | Function 3 |
|---|---|---|---|
| % Variation | 51.49 | 45.99 | 2.52 |
| RH | .08695 | .75432 | .42578 |
| Bulla L | −1.00170 | .46017 | .20980 |
| ML | .91875 | .00085 | −.63020 |
| PAA | .02162 | .08900 | .99334 |

TABLE 12
**Standardized Canonical Discriminant Function Coefficients for *Idiurus zenkeri***

Loadings given for first canonical axis and percentage of variation explained by the axis; see table 3.

| | Function 1 |
|---|---|
| % Variation | 100.0 |
| RH | −.21402 |
| Bulla B | −.48422 |
| RUL | .58284 |
| RLL | .49646 |

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